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THE GENERA OF PHYTOLACCACEAE IN THE SOUTHEASTERN UNITED STATES¹

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PHYTOLACCACEAE R. Brown in Tuckey, Narr. Exped. Congo, 454. 1818,
"Phytolaceae," nom. cons.

(POKEWEED FAMILY)

Herbs, shrubs, vines [or sometimes trees], with lateral expansion normal or by successive cambia. Plants with betalain pigments, rich in saponins (Phytolaccoideae). Sieve-tube plastids usually containing globular crystalloids [these polygonal in *Stegnosperma* and cubic in *Limeum*]. Calcium oxalate mostly

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Special thanks are extended to my brother, James Rogers, for enthusiasm beyond mere tolerance while I collected and observed "*Phytolacca rigida*" during a trip made to North Carolina for multiple purposes. Ihsan Al-Shehbaz, Michel Lelong, James E. Rodman, and Won S. Woo generously helped fill gaps in my information. I am indebted to George Staples for photographing *Trichostigma* in Florida. That Elizabeth Kellogg made available her treatise on Phytolaccaceae prior to its publication in the *Flora of the Lesser Antilles* is acknowledged with gratitude. The late Dorothy H. Marsh, Diane C. Johnson, and Karen Stoutsenberger, supervised by Carroll Wood and/or Kenneth R. Robertson, drew the three illustrations using materials collected in Mississippi, Virginia, and Florida by R. B. Channell, Carroll Wood, and Frank C. Craighead, Jr. Supplementary materials of *Petiveria* came from specimens from Florida in the Harvard University Herbaria (g, h, *Long & Broome 2543*, GH) and Puerto Rico (l–s, *Wagner 1629*, A). Reviews of the manuscript by Carroll Wood and Stephen Spongberg yielded important improvements, and the paper would be poorer if not for Elizabeth Schmidt's editorial talents. Barbara Nimblett moved the project along quickly by helping with the typing.

present as styloids (Rivinoideae) or raphides (Phytolacchoideae, Agdestidoideae) [or spherical aggregates of crystals in Barbeuioideae, Microteoideae, Stegnospermatoideae], and in additional forms. Leaves alternate, simple, entire, usually petiolate, often with crystals bulging on blades (when dry) or appearing as translucent dots; stomata anomocytic or paracytic. Inflorescences mostly racemose, paniculate, or spicate, the rachises sometimes terminated by flowers, frequently bearing simple or compound lateral dichasia; bracts and bracteoles usually small. Flowers perfect [or imperfect], usually actinomorphic (regular), or slightly irregular or zygomorphic, usually with a hypogynous disc. Perianth uniseriate [or biseriate by virtue of petaloid staminodes in *Stegnosperma* and in *Anisomeria coriacea* var. *petalifera* fide Walter], the tepals usually 4 or 5, inconspicuous or infrequently showy, usually greenish or white, separate or slightly [or rarely strongly] coalescent basally, usually persistent. Stamens [3 or] 4 to numerous, in 1 or 2 whorl(s) or inserted irregularly; filaments separate or connate basally; anthers usually elongate. Pollen grains 2- (*fide* Davis) or 3-celled when shed, 3-colpate [3-colporoidate], pantocolpate [or pantoporate], the exine not reticulate, the tectum spinulose and usually punctate-perforate. Gynoecium of 1 to many [apparently separate or] connate, superior (partly inferior in *Agdestis*) carpels, each with 1 style (styles connate in *Agdestis*), 1 locule, and 1 adaxial-basal ovule, this (ana-)campylotropous to (among our genera, *Petiveria*) erect and straight with the micropyle adjacent to the funiculus, in pluricarpellate species the micropyle abaxial to the floral axis [adaxial in *Stegnosperma*]. [Gynoecium compound and unilocular in Microteoideae.] Fruits berries or drupes, or dry and indehiscent [or capsular, or with separate fleshy or dry carpels], sometimes winged by the persistent tepals [or with wing derived from pericarp], barbed or hooked in some genera. Seeds erect, usually compressed and circular to reniform in outline, sometimes elongate (*Petiveria*), lacking arils (or minutely arillate in *Rivina*) [or strongly arillate in *Stegnosperma* and *Barbeuia*]; seed coat usually smooth and dark, sometimes adherent to pericarp. Embryo annular or sharply bent, sometimes plicate. Megagametophyte (embryo sac) of the Polygonum type (deviating slightly in *Rivina*). Endosperm formation initially nuclear. Principal nutritive tissue in mature seed perisperm. (Including Agdestidaceae Nakai, Barbeuiaceae Nakai, Petiveriaceae Agardh, Rivinaceae Agardh, Stegnospermataceae Nakai.) TYPE GENUS: *Phytolacca* L.

A poorly delimited family of about 17 mostly small and often monotypic genera collectively including about 120 species. *Phytolacca*, with about 25 species, is the largest genus; *Seguieria* Loebl. is slightly smaller. Concentrated in the American tropics and subtropics, the family is represented as far north as southern Canada (*Phytolacca americana*); at the southern extreme distributions of about half the genera include or lie within Argentina or Chile. The Old World indigens are *Barbeuia* Thouars in Madagascar, *Monococcus* F. Mueller in and near Australia, *Lophiocarpus* Turcz. in Africa, and species of *Phytolacca* in Africa and Asia. *Petiveria alliacea*, *Rivina humilis*, *Trichostigma octandrum*, *Phytolacca americana*, *Agdestis clematidea*, and the debatably phytolaccaceous *Gisekia pharnacioides* L. (see footnote in key) occur in the area

of the Generic Flora. *Phaulothamnus spinescens* Gray, which may or may not belong in the Phytolaccaceae, ranges as close as Texas.

The Phytolaccaceae, clearly a family of the order Centrospermae (Caryophyllales), is composed of a diverse assortment of usually unarmed herbs, vines, and trees. Members usually have fairly nonsucculent, *alternate leaves* (vs. leaves mostly opposite in Caryophyllaceae, Aizoaceae, and Nyctaginaceae), betalain pigments (rather than anthocyanins as in Caryophyllaceae and Molluginaceae), and usually globular crystalloids in sieve-tube plastids (vs. crystalloids absent in Chenopodiaceae and Amaranthaceae and polygonal in Caryophyllaceae). The *inflorescences are predominantly racemes or racemelike* but are often partly cymose (vs. more distinctly cymose in most relatives or potential members) and bear *unspecialized bracts* (in comparison with those of Nyctaginaceae and Amaranthaceae, and the “sepals” of Portulacaceae). Phytolaccaceous flowers are generally perfect with *nonshowy perianths* (unlike Portulacaceae, somewhat showy in *Agdestis*) composed of *one whorl of basally connate or separate tepals* (tepals or “sepals” connate in Nyctaginaceae and Aizoaceae). Stamens in Phytolaccaceae vary widely in number and arrangement—in some genera they are numerous and inserted irregularly. With exceptions, the stamens are not elaborated into attractive organs (as they are in some Aizoaceae and Molluginaceae and possibly Caryophyllaceae) and tend only slightly toward connation (thus differing from staminal tubes of some Amaranthaceae). The pollen is variable. Most genera have either a *solitary carpel or several carpels with varying degrees of fusion, each carpel typically with a free style, one locule, and one ovule*. (Compound unilocular or partly unilocular ovaries characterize Amaranthaceae, Chenopodiaceae, Portulacaceae, and Caryophyllaceae. With exceptions, Aizoaceae, Caryophyllaceae, Molluginaceae, and Portulacaceae tend to have multiplication of ovules on variously specialized placentas.)

The six subfamilies recognized in Nowicke’s “palynotaxonomic study” (1968) of Phytolaccaceae are congruent with Heimerl’s (1934) five tribes and one set of anomalous genera. In the principal revision prior to those of Nowicke and Heimerl, Walter (1909) divided a more broadly circumscribed Phytolaccaceae into two subfamilies, three tribes, and two subtribes. All three monographers perceived *Anisomeria* D. Don, *Ercilla* A. Juss., and *Phytolacca* to constitute a coherent assemblage. This trio, which is characterized by raphides and multiple carpels with as many locules and styles, makes up the entire Phytolaccaceae *sensu* Hutchinson and the entire subfam. Phytolaccoideae in Nowicke’s treatment. Walter, Heimerl, and Nowicke agreed further on the boundaries of the group now known as subfam. Rivinoideae Nowicke,² characterized by styloid crystals and flowers with single carpels.

²With their authorships brought into accordance with the 1983 International Code of Botanical Nomenclature, the tribes Nowicke recognized under subfam. Rivinoideae are Seguierieae Moq. (two extralimital genera with paniculiform inflorescences and samaroid fruits) and Rivineae Endl. (seven genera, including our *Petiveria*, *Rivina*, and *Trichostigma*, with spikes or racemes and nonsamaroid fruits). Although some botanists attributed C. A. Agardh with the authorship of tribe Rivineae in his *Aphorismi Botanici*, he evidently published Rivineae as an “order” nomenclaturally equivalent to a modern family (see Agardh, p. 61, and ICBN, 1983, Art. 18.2).

The affinities of the remaining members or potential members of the family have spawned disagreement and remain unsettled. Subfamily Microteoideae Eckardt ex Nowicke is made up of *Lophiocarpus* and *Microtea* Sw. in Nowicke's classification. Walter did not include *Lophiocarpus* in the Phytolaccaceae and listed *Microtea* under *genera anomala*. Heimerl listed both as anomalous. Both Heimerl and Walter placed the three genera corresponding to Nowicke's subfamilies Barbeuioideae Nowicke, Agdestidoideae Nowicke, and Stegnospermatoideae H. Walter in the Phytolaccaceae at various infrafamilial ranks or among *genera anomala*. Other botanists have excluded them from the Phytolaccaceae as *incertae sedis* or as distinct families.

Heimerl, Nowicke, and most recent authors departed from Walter and from Dahlgren and colleagues by treating *Achatocarpus* Triana and *Phaulothamnus* Gray together as the family Achatocarpaceae. They further disagreed with Walter by excluding Gyrostemonaceae from Phytolaccaceae. Evidence that the former is out of place even in the Centrospermae comes from palynology, floral morphology, cytology, chemistry, and the nature of sieve-tube plastids and vacuoles in companion cells (Behnke, 1977; Goldblatt *et al.*; Keighery).

The foregoing historical sketch underscores the need for new research aimed toward a better circumscription of the Phytolaccaceae. The confusion comes largely from the fact that to some degree the family comprises the *taxonomic* residue left after the other Centrospermae are sorted into separate families based on apparent specializations. (From here it is a small jump to the common perception of the family as a *phylogenetic* residue left after the evolutionary radiation of other Centrospermae.) An ostensible shared absence of derived distinctions, leaving suspected ancestral traits as similarities, is at best flimsy evidence for phylogenetic relationship.

Yet, even if the family Phytolaccaceae is a repository for residual unspecialized traits, past authors have probably overemphasized its primitiveness. Thus, a few apparently derived characters should be mentioned. Rohweder's conclusion that ovaries in *Phytolacca* separate by bulging from an ontogenetically originally syncarpous region raises the possibility that near-apocarpy in subfam. Phytolaccoideae is phylogenetically secondary. This challenges the hypotheses that the occurrence of near-apocarpy in the Phytolaccaceae is a tie to apocarpous Ranales (see Buxbaum, 1961), and that this condition reflects the starting point for gynoecial evolution in the rest of the Centrospermae. As a second example, the racemes and racemelike inflorescences that predominate in the Phytolaccaceae are interpretable as having evolved by reduction from cymose inflorescences. Cymose arrangements characterize most other Centrospermae and a minority of Phytolaccaceae (mostly peripheral groups), and racemose inflorescences in the Phytolaccaceae (e.g., species of *Phytolacca*) sometimes have dichasial branches. (For an argument that the general evolutionary trend proceeds in this direction, see Stebbins.) To add a third example, Cronquist doubted that the phytolaccaceous trait of one ovule per carpel is primitive in the Centrospermae. Lastly, recent authors have noted that it is simpler to postulate that the betalain pigments of Phytolaccaceae and most other centrosperms are derived than to interpret their presence as ancestral in the order. The latter interpretation requires acceptance of the anthocyanins in Molluginaceae and Caryophyllaceae as arising anew via reversal.

Specializations are to be expected, and these do not rule out a more or less central position for Phytolaccaceae in the Centrospermae. Support for this position appears in apparent spokelike links to disparate satellite groups and centrospermous families through morphological similarities and transitional genera. As examples of the latter, *Stegnosperma* Benth forms a much-discussed bridge to Molluginaceae or Caryophyllaceae, and *Lophiocarpus* and *Microtea* have repeatedly been mentioned as ties to Chenopodiaceae and Amaranthaceae. *Gisekia* resembles species of Phytolaccaceae in having raphides, betalains, and gynoecea that agree developmentally, but it leans toward Molluginaceae in habit, cymose inflorescences, androecial morphology, nectaries, and embryology. (For comparative details see Bogle; Hofmann, 1973; Mabry *et al.* Note that Ehrendorfer, 1976b, placed *Gisekia* in Aizoaceae.)

The structures termed stipules in literature on Phytolaccaceae are probably prophylls in some, if not all, genera in which they occur (Eckardt, 1964; see also Buxbaum, 1949). In *Petiveria alliacea* stipulelike axillary emergences can be seen to be attached like reduced leaves to developed axillary shoots, and multiple pairs of emergences appear to correspond to multiple axillary shoots.

According to the sketchy data on hand, chromosome numbers in Phytolaccaceae range as polyploids, but not aneuploids, from $2n = 18$ to $2n = 108$. (Keighery provided a survey.)

Most economic uses for members of the Phytolaccaceae appear in the generic treatments. Among extralimital genera *Ercilla spicata* (Bert.) Moq. is a minor ornamental, while species of *Anisomeria*, *Gallesia* Casar., *Hillieria* Vell., *Microtea*, and *Seguieria* find uses in folk remedies. Roots of *Stegnosperma scandens* (Lunan) Standley serve as a soap in Mexico (Standley & Steyermark).

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KEY TO THE GENERA OF PHYTOLACCACEAE IN THE SOUTHEASTERN UNITED STATES

- A. Carpel 1; stigma 1; style 1 or absent; crystals predominantly styloids.
 - B. Inflorescences spicate or nearly so; flowers distinctly zygomorphic; ovaries densely pubescent; fruit dry, cuneiform, armed with 4 or more hooks at apex; seed much longer than wide. 4. *Petiveria*.
 - B. Inflorescences racemose; flowers actinomorphic or nearly so; ovaries glabrous or glabrate; fruit fleshy, rounded in outline, unarmed; seed more or less lenticular.
 - C. Plants usually herbs or subshrubs (sometimes scandent); leaf blades often deltoid; stamens 4; style well developed, stigma capitate or lobed; fruit bright red or orange; seed covered with “hairy” remnant of pericarp (this sometimes wearing off, leaving bare seed coat). 3. *Rivina*.
 - C. Plants usually robust woody vines, sometimes somewhat arborescent; leaf blades ovate or lanceolate to elliptic; stamens 8 or more; style absent or

- inconspicuous, stigma penicillate; fruit black or dark reddish; seed bare or covered with "nonhairy" remnant of pericarp. 2. *Trichostigma*.
- A. Carpels usually 4 or more, apparently apocarpous or syncarpous; stigmas and styles usually 4 or more (except *Agdestis*, with solitary style crowned with usually 4 conspicuous stigmas); crystals predominantly raphides.
- D. Plants climbing vines; leaf blades mostly cordate, often about as long as wide; ovary partly inferior, syncarpous and usually 4-locular (becoming unilocular in fruit by abortion); style solitary; fruit dry, only 1 per flower (not an aggregate). 5. *Agdestis*.
- D. Plants nonclimbing herbs; leaf blades linear-oblong to elliptic or ovate, longer than wide; ovary superior, apparently apocarpous with 5 carpels or syncarpous with usually 10 carpels and locules; styles as many as carpels; fruit baccate or an aggregate of nutlets.
- E. Leaves alternate, usually separated by well-developed internodes, usually wider than 1 cm; inflorescence racemose, uncrowded; stamens usually 10; gynoecium syncarpous, carpels usually 10; fruit baccate. 1. *Phytolacca*.
- E. Leaves often opposite or subopposite, sometimes clustered at nodes, narrower than 1 cm; inflorescence fundamentally cymose, more or less umbelliform and fasciculate, crowded; stamens 5; gynoecium apparently apocarpous, carpels 5; fruit an aggregate of warty nutlets. [*Gisekia pharnacioides* L.³]

Subfamily PHYTOLACCOIDEAE

1. *Phytolacca* Linnaeus, Sp. Pl. 1: 441. 1753; Gen. Pl. ed. 5. 200. 1754.

Large, perennial [or sometimes annual?], erect [or scandent or procumbent], often shrublike herbs [*Phytolacca dioica* and *P. Weberbaueri* becoming large trees], expanding laterally by successive cambia [or *P. Meziana* with a continuous ring of secondary xylem *fide* Wheat]. Stems and axes of inflorescences often purplish or reddish, the pith diaphragmed [or absent] in mature stems. Patterns of growth monopodial or sympodial, the branching frequently pseudodichotomous, sometimes with multiple shoots emerging from one leaf axil. Taproots often large (reaching several dm in diameter in *P. americana*). Plants mostly glabrous, frequently scurfy-puberulent on axes of inflorescences [and infrequently elsewhere]. Raphide bundles usually bulging on dried specimens. Leaves petiolate [or nearly sessile], the blades thin to slightly succulent, often crisped-undulate, usually elliptic (often narrowly so) to ovate or lanceolate, mostly variously pointed apically, often asymmetric and usually tapered and decurrent onto the petiole basally; stomata anomocytic. Inflorescences terminal, often overtopped by axillary growth, then usually borne opposite a leaf or nearly so [infrequently axillary or arising from old growth], pedunculate [or nearly sessile], nodding to erect, the straight central rachis bearing numerous radiating much shorter [to virtually absent] pedicels, each of these subtended by a scarious elongate bract and bearing 2 small bracteoles, these sometimes subtending second- [or third-]order axes, especially toward the inflorescence base. Flowers small, perfect [or imperfect, the plants dioecious, probably infrequently polygamous], actinomorphic or nearly so. Perianth uniseriate, with 5 [rarely 3 or 4], white to pink or reddish [or yellowish, greenish, or purple],

³Adventive in our area. Bogle treated *Gisekia* for the Generic Flora under Molluginaceae.

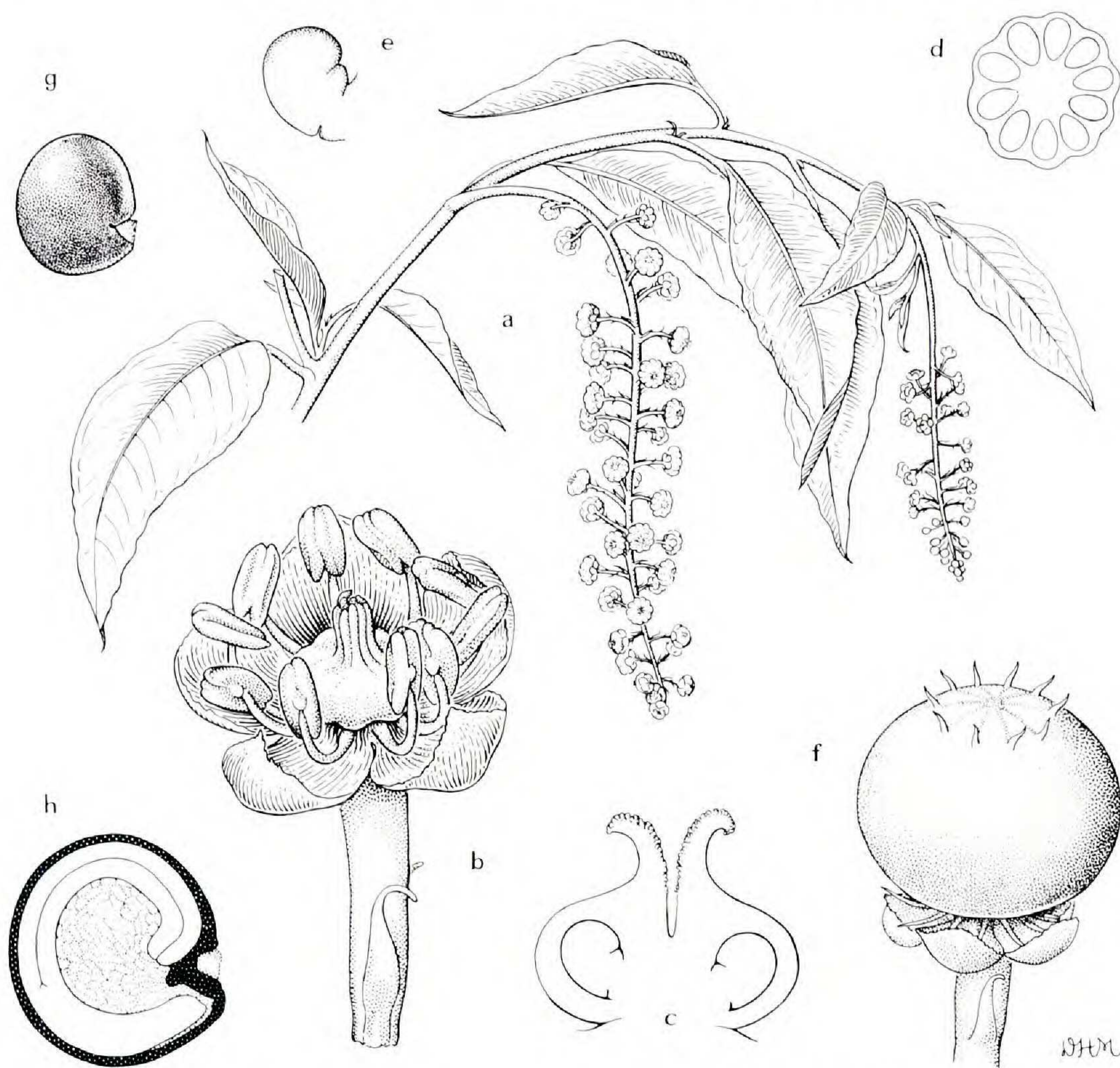


FIGURE 1. **Phytolacca.** a–h, *P. americana*: a, branchlet with flowers and immature fruits, $\times \frac{1}{2}$; b, flower, stigmas not yet receptive, $\times 8$; c, gynoeceum with receptive stigmas, semidiagrammatic, vertical section, 2 ovules visible, $\times 15$; d, gynoeceum, diagrammatic cross section, with ovule filling each locule, $\times 10$; e, ovule, lateral view, micropyle below, $\times 22$; f, mature fruit, $\times 3$; g, seed, lateral view, funicular remnant to right, $\times 5$; h, seed in section, semidiagrammatic, seed coat black with white stipples, embryo unshaded, perisperm in center, $\times 8$.

broad, entire or erose, persistent [or caducous], separate or nearly separate tepals. Stamens [ca. 5 to] usually 10 in *P. americana* [to ca. 33], usually in 1 [or 2] series; filaments distinct [or connate basally], broadened at the bases [to filiform]; anthers dorsifixed. Pollen grains prolate to spheroidal, 3-colpate, the tectum spinulose and punctate-perforate. Gynoeceum usually of 10 [or ca. 5 to ca. 17] connate [to nearly distinct] carpels arranged in a ring, each bearing a recurved to erect style with the stigmatic surface decurrent adaxially. Fruit a smooth globose to depressed berry (sulcate when dry), usually 10-locular (*P. americana*) [or carpels remaining separate], usually bearing the styler remnants, purple-black [or reddish]. Seeds usually 10 (*P. americana*), nearly circular to lopsided reniform [to obovate], flattened, the testas hard and shining, black or nearly so except for light-colored funicular remnants. Embryo annular. Endosperm persisting as a vestige in the mature seed. $2n = 18, 36, 72$. (Including

Sarcoca Raf., *Pircunia* Moq.). LECTOTYPE SPECIES: *P. americana* L. (*P. decandra* L.); see Britton & Brown, Fl. No. U.S. Canada, ed. 2. 2: 26. 1913. (Name from Greek *phyton*, plant, and *lacca*, a Latinized reference to the pigment variably known as lake, lac, or laque.) — POKE,⁴ POKEBERRY, POKEWEED.

Approximately 25 species in three subgenera⁵ of two sections each, distributed mostly from southeastern Canada, southward throughout most of North, Central, and South America, and in the West Indies. In the Old World a small number of species range from Africa and Madagascar into Asia Minor and eastward across southern Asia to Korea, Japan, and Taiwan. The unusually wide range of *Phytolacca acinosa* Roxb. (*P. esculenta* Van Houtte), from Pakistan to Japan and elsewhere, is no doubt partly attributable to its culinary history. *Phytolacca dodecandra* L'Hér. is widespread in Africa. *Phytolacca americana*, *P. icosandra* L., *P. octandra* L., and *P. purpurascens* A. Br. & Bouché are adventive in scattered, usually warm regions worldwide. Outside of our area, but in the United States, *P. brachystachys* Moq. is Hawaiian; *P. heterotepala* H. Walter, an otherwise Mexican species, appeared in San Francisco, California (Howell); and *P. dioica* L. is grown in California.

Sect. PHYTOLACCA (flowers perfect) of subg. PHYTOLACCA (carpels completely connate, styles more or less connivent) is represented in the southeastern United States by *P. americana*, $2n = 36$, which occurs in southern Quebec and Ontario, in every state of the United States east of or intersected by a longitudinal line crossing eastern Nebraska, and in northeastern Mexico. Populations in Arizona, Oregon, and California probably started from introductions by humans. *Phytolacca americana* is widely scattered adventively in the Old World.

A possible second species in our area, *Phytolacca rigida* Small inhabits seaside habitats from North Carolina to Texas and extends inland across much of Florida and into Alabama (Harper). Authors are divided as to whether *P. rigida* ought to be recognized as distinct from *P. americana*. The most salient distinguishing feature of the former, infructescences remaining erect (vs. usually nodding), proved to have a genetic basis in the transplant experiment reported by H. J. Rogers. A second conspicuous difference is that *P. rigida* has somewhat succulent leaves, a distinction undermined by Lloyd's (1914) demonstration of plasticity in leaf thickness in *P. "decandra"* (*P. americana*). My own observations complicate evaluation of this character.⁶

⁴"Poke" is thought to come from "pocan" or "puccoon," probably an Algonquin term for a plant that contains dye.

⁵*Phytolacca* subg. *Pircunia* (Moq.) H. Walter is a later homonym of *Phytolacca* subg. *Pircunia* Poeppig & Endl. (Nov. Gen. 1: 26. 1836, two species now placed in *Anisomeria*). Sections "*Pircunia*" and "*Pircuniopsis*" should be called by their older names, sects. *Pircuniastrum* and *Pseudolacca*, due to changes in the International Code of Botanical Nomenclature since Nowicke's revision. These appeared as sections of the genus *Pircunia* in Moquin-Tandon (1849) and as sections of *Phytolacca* in Baillon (1872). (Section "*Pircunia*" also contradicts Art. 64.3.)

⁶In August, 1983, I observed *Phytolacca rigida* and *P. americana* at Emerald Isle, Carteret County, North Carolina, represented at A by *G. Rogers* 107 and 108. Plants of *P. rigida* at that locality had thick leaves, while those of *P. americana* nearby were thin, suggesting genetic difference. But indicating plasticity, two young plants of *P. rigida* (seeds from my no. 107) have leaves only barely perceptibly thicker than two plants of *P. americana* (seeds obtained inland in Massachusetts) of the same age in

Selected additional differences are that *Phytolacca rigida* tends to have narrower leaves with more gradually tapered bases (which held up on the potted plants), shorter inflorescences bearing fewer flowers, broader bracteoles, shorter pedicels (often shorter than the fruits), and peduncles with vascular cylinders of smaller diameter but with thicker xylem (broader sampling needed). Hardin compared *P. americana* and *P. rigida* in detail, and my comparison leads me to agree that differences between the two taxa are blurred by overlap. Perhaps *P. rigida* would be best recognized at the varietal level. The combination remains to be made.

Phytolaccas are usually large herbs (or even trees) often having reddish axes, pseudodichotomous branching, diaphragmed pith, and conspicuous raphide bundles. The inflorescences are usually pedunculate, cylindrical, racemose (although often with lateral dichasia toward the base), fundamentally terminal, and displaced laterally by axillary growth. (Inflorescences in *Ercilla* usually are nearly sessile, more or less spicate, and axillary, with those of *Anisomeria* condensed and more obviously terminal.) Species of *Phytolacca* usually have five small, nonshowy, thin, and nearly equal tepals (vs. tepals fleshy and unequal in *Anisomeria*). Five to more than 15 carpels range from near apocarpy to pronounced syncarpy. In most species these mature into a reddish to black berry containing numerous flat, blackish seeds. (The 5(–8) or fewer carpels of *Anisomeria* and *Ercilla* usually remain separate.)

Nowicke (1968) noted that interspecific hybridization, infraspecific variation, and apparent weak genetic control of many qualitative characters have obscured boundaries between species.

A familiar weed, *Phytolacca americana* is a tolerant pioneer in disturbed sites but a poor competitor when young. Evidently limited to the north mainly by summer temperatures and to the west by dry conditions, the perimeter of the range of this species has possibly changed little in response to human activity. Nevertheless, it has certainly escaped from scattered habitats, probably mostly along streams, where the taproot has been observed to withstand flooding, to places disturbed by humans. Fassett & Sauer concluded that ecological disruption in Colombia broke down barriers between *P. rugosa* A. Br. & Bouché and *P. rivinoides* Kunth & Bouché. (This paragraph based largely on Sauer, 1952.)

The ability of pokeweeds to become established quickly far from parental plants upon disturbance of soil and vegetation draws attention to their seeds. These remain viable in fecal deposits from birds, which undoubtedly are the primary agents of dispersal (Edmisten, Armesto *et al.*). Shown to withstand burial for almost 40 years (Toole & Brown), the seeds germinate in response to a complex set of factors or to artificial scarification. Farmer & Hall found

the same pot indoors in Cambridge, Massachusetts. (It must be stressed that my observations on potted specimens are preliminary, based on a small number of specimens only a few inches tall.) Detracting further from the significance of succulent leaves, I have seen seaside plants of *P. americana* with thickened leaves in Hudson County, New Jersey, and Plymouth County, Massachusetts (*G. Rogers* 109 and 110). Plants with thickened leaves tapering at the base and with horizontal to erect inflorescences occur on Nantucket Island, Massachusetts (C. E. Wood, obs. July, 1984).

the inability of fairly fresh seeds to sprout in the dark to be largely overcome by stratification, although a functional dimorphism appeared since some seeds required light even after stratification. Seeds from one or from different individuals responded variably to a given combination of conditions (Farmer & Hall, Armesto *et al.*). Thus, longevity, efficient translocation, and nonuniform requirements for germination allow pokeweed seeds to be delivered to and/or to await disturbances, ensuring continued production of seedlings despite environmental vagaries.

Armesto and colleagues interpreted the ample fruit set of *Phytolacca americana* as a sign of autogamy; the same observation plus release of pollen followed by partial breakdown of stigmas before anthesis led Meehan to the same conclusion.

Young shoots or leaves from *Phytolacca* “*esculenta*” (*P. acinosa*), *P. americana*, and other phytolaccas can serve as food after being boiled once or twice to deactivate toxins. American Indians ate *P. americana*, and it remains a favorite wild delicacy commonly served as poke salad or “sallet.” It has even been marketed canned. However, pokeweed believed to have been properly prepared sickened a group of campers, according to a report cited by Edwards & Rodgers, and contemplation of the potency of pokeweed mitogens (discussed below) may dishearten would-be enthusiasts. Despite their toxicity, pokeberries have filled pies and have colored confections and wines (Braun; Shultz; Sauer, 1950). Renewed interest in derivation of food coloring from *Phytolacca* hinges on removal of offensive substances (e.g., see Driver & Francis, Forni *et al.*). The berries have also been employed as sources of ink, as rather poor dyes for fabrics, and (at least in certain extralimital species) as a substitute for soap. *Phytolacca americana* and other species have served in the Old World as ornamentals. The principal shade tree of the Argentinian pampas, *P. dioica* (*ombú* or *bella sombra*), is planted in warm, dry regions.

A formidable brew of bioactive compounds in all parts of the plants clearly lies behind most remaining roles of *Phytolacca* in human affairs, including its use as a narcotic and as a medicine in both hemispheres. (For amplification of the rich medicinal history of *P. americana*, see Byrd; Shultz; Sauer, 1950; and Steinmetz.) Even though remedies incorporating phytolaccas are obsolete, their bioactivity remains of interest as outlined in the paragraphs that follow.

Phytolacca americana is a common and conspicuous toxic hazard. From the use of the root as a medicine and from its being mistaken at times for horseradish or parsnip, the drastic and sometimes fatal consequences of eating it are well known (Ahmed *et al.*; Anonymous; Guthrie; Jenkins; Macht; Sauer, 1950; Shultz). The threat extends to farm animals, especially pigs, which occasionally dig out lethal quantities (Barnett, Hansen, Patterson). The colorful berries are dangerous, too, although they affect various people differently. In gathering data on ca. 100 ingestions of pokeberries, O’Leary uncovered only two mentions of human fatalities. One was a two-year-old child in Rhode Island (whose case Kingsbury discussed in 1980). The other is Chesnut’s old report that fruits or seeds are held to blame for deaths of a “few” children. As related in a second-hand report in Wood & Bache, a double handful killed a woman following purgation, prostration, and coma. Hansen recorded with no

elaboration another fatality from the berries; and Hardin & Arena documented the death of a five-year-old girl who drank a beverage made from the berries. On the other hand, Hardin & Arena asserted that a small number of berries is generally harmless to adults and older children. Shultz likewise noted that some people eat pokeberries with no harm, but cautioned that this is not usually the case and mentioned gastrointestinal distress suffered by others after dining on birds fed pokeberries. Individuals from a group of Boy Scouts in Kentucky variously had diarrhea, cramps (possibly due to a different cause), or no symptoms after a meal of pokeberry pancakes and some raw berries (Edwards & Rodgers).

In addition to gastric irritation, symptoms of poisoning by *Phytolacca* berries in humans include hematological alterations and probably depression of the central nervous system with inhibition of the heart and respiration, mental aberrations, and convulsions. The three last symptoms have been induced in various experimental animals by the berries and are brought about in humans by poke root. Handling plants of *Phytolacca americana* and other species may cause dermatitis (Sauer, 1950). Relating the toxicity of *Phytolacca*s to their chemistry demands continued research on the classes of bioactive compounds discussed individually below; the high concentrations of oxalic acid and contradictory reports concerning alkaloids (*cf.* Ahmed *et al.*, Goldstein *et al.*, Jack & Rogers, Jenkins, Lascombes & Bastide, Steinmetz, Wall *et al.*, L. Webb) should not be overlooked.

A rich array of triterpenoid saponins and their free nonsugar (aglycone) components occurs in roots, fruits, and other parts of species of *Phytolacca*. In several papers, Woo, Kang, and collaborators reported ten "phytolaccosides," along with the structures of some, in *P. americana* and other species. Similarly, Suga and colleagues detected and in some cases determined structures for over eight saponins in roots of *P. americana* and concluded that the "phytolaccatoxin" of earlier literature was a mixture of more than three saponins. The principal aglycone in *P. americana* is evidently the triterpenoid phytolaccagenin; others include phytolaccagenic, jaligonic, and esculentic acids. Saponins from berries of *P. dodecandra* have aroused interest as biodegradable, ostensibly fairly safe, locally producible molluscicides for controlling schistosomiasis (Lemma, Parkhurst).

A set of single-chain and polymeric proteins associated with carbohydrates, designated mitogens⁷ due to their ability to stimulate mitotic proliferation following morphological alteration of lymphocytes, has also received much attention in literature concerning the chemistry of *Phytolacca*. Certain mitogens

⁷Mitogens from *Phytolacca*s belong to the class of proteins and glycoproteins known as lectins, compounds that bind sugars specifically and agglutinate cells or precipitate sugar-containing compounds. A mitogenic lectin mimics the immunological effect of an antigen by stimulating T- and/or B-lymphocytes. That is, an antigen induces lymphocytes to enlarge into blast cells and proliferate. T-lymphocytes do so directly in response to the antigen, whereas effective contact between B-lymphocytes and antigen is usually mediated by T-lymphocytes. Stimulated B-lymphocytes differentiate into plasma cells and secrete antibodies. Stimulation by mitogenic lectins differs from that of antigens in that mitogens indiscriminately activate large numbers of lymphocytes.

from *Phytolacca* stand out among plant mitogens due to their high potency and/or ability to act upon B-lymphocytes as well as T-lymphocytes. Waxdal (1974) characterized a set of mitogens from *P. americana* as Pa-1 to Pa-5, among which Pa-2 probably corresponds to, or is the chief component of, the original commercially available "pokeweed mitogen" or "PWM." The dangers of pokeweed mitogens to humans are unclear. Accidental exposure to juices from *P. americana* via ingestion, breaks in the skin, and the conjunctiva has brought about hematological changes in numerous people, including researchers studying this species (Barker *et al.*, 1965, 1966, 1967a, 1967b). (A brief review of research on pokeweed mitogens appears in Waxdal, 1978.)

Like many other plants, species of *Phytolacca* contain antiviral proteins. Having been detected early in the course of research on viral inhibitors in plants, and being unusually potent, pokeweed antiviral peptide (PAP) has received special attention. PAP blocks the reproductive cycle of exceedingly diverse viruses in equally diverse hosts, at least in part by interfering with protein synthesis on the hosts' ribosomes. Coupled with an antibody, PAP may serve as a selective antitumor agent (Masuho *et al.*). (For a sampling of the extensive literature concerned with PAP, see Grasso & Shepherd, Irvin, Owens *et al.*, Tomlinson *et al.*, and Ussery *et al.*). A second antiviral protein from *P. americana* recently characterized by Irvin *et al.* is called PAP II.

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Subfamily RIVINOIDEAE Nowicke

Tribe RIVINEAE Endl.

2. *Trichostigma* A. Richard in Sagra, Hist. Fis. Cuba **10**: 306. 1845.⁸

Climbing, shrubby, or somewhat arborescent woody plants, without successive cambia (*Trichostigma octandrum*, stems to 15 cm thick in this species). Plants glabrous or puberulent to hirsute-pilose on young stems, leaves, petioles,

⁸This work was issued in French (*Trichostigma*, p. 627, 1851?) and evidently a second time in Spanish (*Trichostigma*, 2: 306. 1853!).

and inflorescence axes. Calcium oxalate present primarily as styloid crystals. Leaves petiolate, the blades sometimes crisped-crenulate, ovate or lanceolate to elliptic, usually pointed and sometimes apiculate apically, mostly cuneate to rounded [or cordate] basally. Racemes borne at ends of minor (or sometimes major) leafy branches or axillary [sometimes displaced by sympodial growth to a pseudolateral position in *T. peruvianum*], sometimes clustered, axes becoming reddish, the slender central rachises bearing many shorter pedicels, each subtended by and usually adnate to one subulate, deciduous or persistent bract and bearing a pair of minute bracteoles. Flowers perfect, fragrant, with 4 subequal, concave, whitish to yellowish or greenish (becoming reddish with age) [sometimes reported as brownish or externally brownish in *T. peruvianum*], separate, oblong-elliptic or tapered tepals, these reflexed or spreading in fruit. Stamens 8–13 (rarely more) [–many]; filaments $\pm$ filiform; anthers linear, cleft at the bases. Pollen grains subprolate to spheroidal, mostly 3-colpate [or 11- to 15-colpate], the tectum spinulose. Gynoecium unicarpellate and unilocular; ovary subglobose to elliptic or flask shaped, compressed; style absent or very short, stigma penicillate. Fruit fleshy, nearly globose, black or reddish. Seed lenticular, often plump, dark, glossy and bare or with adherent pericarp tissue. (*Villamillia* Ruiz & Pavon,⁹ *Villamilla* Auct.) TYPE SPECIES: *T. rivinoides* A. Richard, nom. illegit. (= *T. octandrum* (L.) H. Walter, *Rivina octandra* L.). (Name from Greek *trichos*, hair, and *stigma*, in reference to the brushlike stigma.)

A small genus of three species distributed throughout most of tropical America. *Trichostigma polyandrum* (Loes.) H. Walter (*Rivina polyandra* Loes.) is found in rain forests from southern Nicaragua to western Panama (for a recent treatment see Burger). Limited to Peru and Ecuador, *T. peruvianum* (Moq.) H. Walter likewise inhabits shady forests, possibly favoring rocky sites. *Trichostigma octandrum* ranges from Argentina northward across South and Central America and the West Indies to a sparse representation in Florida only as far north as Collier County (Big Cypress National Preserve, Chokoloskee Island) and Dade County.

Trichostigma octandrum is variously described as a vine, a shrub, or rarely a tree. Numbers of stamens, shapes of tepals, and lengths of racemes fluctuate. Individuals of this species are frequently markedly pubescent, a condition that prompted Kitanov to propose “*T. octandrum* forma *hirsutum*” from Cuba, where this tendency is pronounced. *Trichostigma octandrum* and *T. peruvianum* differ from *T. polyandrum* in having 12 or fewer stamens (vs. over 20) with filaments usually longer than 1.2 mm and (in *T. octandrum*) persistent in

⁹*Villamillia tinctoria* Ruiz & Pavon, Fl. Peru. Chil. 4: pl. 402! (= *Trichostigma peruvianum*) entered the botanical literature among a set of plates distributed sometime before 1830 and thus prior to Richard's publication in 1845 of *Trichostigma* and its generally acknowledged type species. According to the 1983 International Code of Botanical Nomenclature, Art. 42, the names of a genus and a species “may be” simultaneously validated, and a plate published before 1908 with analysis “is acceptable” for that purpose (the plate in question contains analysis as explicitly defined therein). I have not accepted *Villamillia tinctoria* as validly published, which appears to be an option implied in the wording of the article.

fruit (vs. under 1 mm and not persistent). Racemes in *T. octandrum* only rarely attain 15(–20) cm in length—those of *T. peruvianum* usually exceed 20 cm, and lengths in *T. polyandrum* are intermediate. Large leaves cordate at base distinguish *T. peruvianum* from its congeners.

Trichostigma is most similar to *Rivina*, in which earlier botanists included all three species, a placement that Burger thought perhaps to be best, although he did not formally merge the genera. A number of characters distinguish the two. *Trichostigma*s tend to be shrubs or robust climbers to several meters tall with ovate or lanceolate to elliptic leaf blades, as opposed to the herbaceous or suffrutescent, sometimes vinelike *Rivina*, which only rarely grows as tall as two meters and often has deltoid leaf blades. Flowers of *Trichostigma* have 8 to many stamens (vs. 4 in *Rivina*) and sessile or nearly sessile penicillate stigmas (vs. capitate on well-defined styles in *Rivina*). In contrast with Buxbaum's (1955, pp. 209, 210) mention of indument on seeds of *Trichostigma* ("*Villamilla*"), a well-known peculiarity of *Rivina*, I found no "hairy" seeds in any of the three species of *Trichostigma* (herbarium specimens at A and GH). Some seeds of *Trichostigma* do resemble those of *Rivina* in remaining covered by pericarp tissue after most of the flesh of the fruit falls away. With corroborative survey needed, secondary growth in *Trichostigma* is normal and sometimes accumulates massively, unlike the weaker anomalous secondary growth of *Rivina*, which reportedly occurs in thick stems (Metcalf & Chalk; Walter, 1909; specimen of *T. octandrum*, Abbott 1083, GH). The sole chromosome count for *Trichostigma*, $2n = 72$ for *T. peruvianum*, is two-thirds of the $2n = 108$ reported repeatedly in *Rivina*.

The extensive distribution of *Trichostigma octandrum* is matched by its ecological breadth. In Florida this species grows in or on the margins of hammocks, on swampy ground, on disturbed sites, and in moist woods. Among the habitats throughout its range are gallery forests along tropical rivers, wet evergreen forests, tropical swamps, coastal grassy areas, coastal *Laguncularia* formations, tidal flats, limestone outcrops, and dunes. Rocky and scrubby places predominate, and ruderal sites are not infrequent.

Trichostigma is palynologically heterogeneous. Nowicke (1968) described grains of *T. octandrum* as 3-colpate and those of the other two species as having five colpi at each pole and five more at the equator. Acetolyzed grains from one collection of *T. octandrum*¹⁰ are mostly 3-colpate, but infrequently have four equatorial colpi; they sometimes have extra, perpendicular, polar apertures, thereby approaching grains as described from the other species. Instead of a total of 15 colpi, Bortenschlager counted 12 arranged like the edges of a cube on pollen from *T. peruvianum*.

My observations fail to confirm the presence of minute, deciduous stipules in *Trichostigma* sporadically mentioned in the literature.

Uses of *Trichostigma* are few. In Colombia leaves of *T. octandrum* have been applied to wounds, and in Haiti a decoction of the leaves has been used to counter suffocation or choking. The thin, flexible stems find applications in

¹⁰Harvard Palynological Collection, slide 6300, Panama, 1940.

basketry and as barrel hoops in the West Indies (Marie-Victorin & León, Morton, Standley). Fruits of *T. peruvianum* have been used for coloring linen, and the dense wood is suitable for handles (Ruiz & Pavon).

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3. *Rivina* Linnaeus, Sp. Pl. **1**: 121. 1753; Gen. Pl. ed. 5. 57 (“*Rivinia*”). 1754.

Often highly branched, perennial (or probably occasionally annual), sometimes scandent herbs, subshrubs, or shrubs, thickening by successive cambia especially at the base, the thin stems with single xylem cylinders. Pattern of branching frequently pseudodichotomous, often with 3 or more shoots arising from 1 node (such branching often taking the form of an inflorescence or vegetative branch, frequently abortive, centered between $2 \pm$ equal divaricate branches). Plants glabrous or scurfy to densely pilose or hispid(ulous) on most organs. Calcium oxalate present primarily as styloid crystals. Leaves alternate or infrequently subopposite, petiolate, the blades usually elliptic or lanceolate to deltoid, generally acuminate apically, the bases usually acute to truncate; stomata rubiaceous or anomocytic. Inflorescences at ends of branches or axillary-lateral, narrow racemes with short pedicels radiating from elongate, straight, central rachises; bracts lanceolate or subulate, bracteoles 2 per pedicel, minute. Flowers perfect. Tepals nearly equal, 4, lingulate to elliptic or oblanceolate, upright to reflexed in fruit. Stamens 4, alternating with and shorter than or about as long as tepals; filaments filiform; anthers oblong-elliptic,

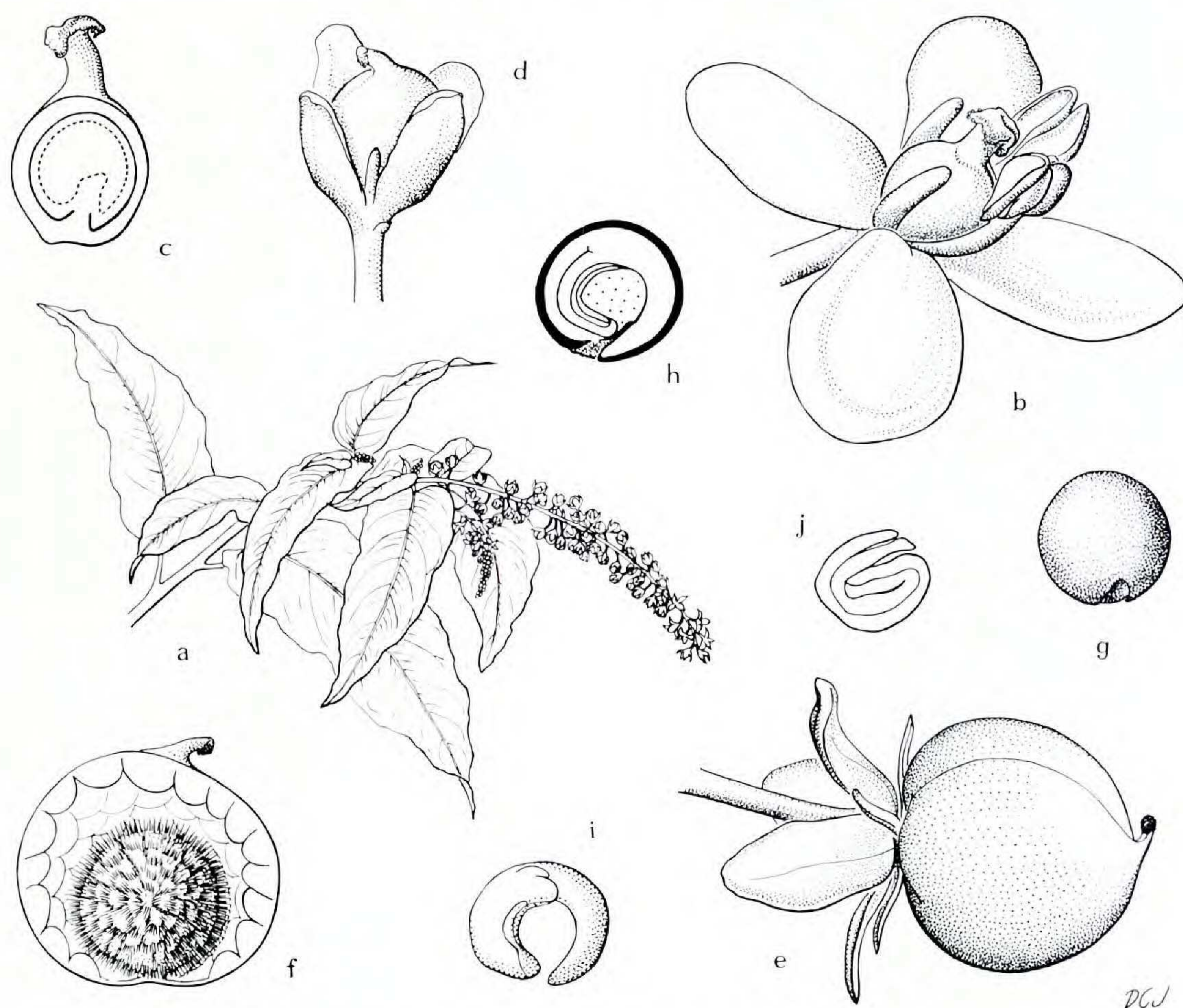


FIGURE 2. **Rivina**. a-j, *R. humilis*: a, tip of flowering shoot, $\times \frac{1}{2}$; b, flower, 2 anthers removed, $\times 12$; c, gynoecium in vertical section—note basal ovule, $\times 6$; d, very young fruit, $\times 6$; e, mature fruit, $\times 6$; f, mature fruit, longitudinal section, note hairy endocarp, fleshy mesocarp, and liquid-filled space between mesocarp and endocarp—note that “bumps” in mesocarp fit into “areoles” on very thin endocarp, $\times 6$; g, seed, $\times 6$; h, seed in vertical section, radicle of embryo at micropyle, perisperm stippled, $\times 6$; i, embryo, oriented as in “h,” $\times 6$; j, section through center of cotyledons of embryo, oriented as in “i,” $\times 12$.

dorsifixed. Pollen grains spheroidal to prolate, the tectum spinulose. Gynoecium unicarpellate; ovary superior, unilocular, compressed, nearly circular to elliptic in outline, grooved adaxially; style filiform, inserted obliquely, (sub)terminal to distinctly eccentric, curved, shorter than to about as long as the ovary; stigma capitate, sometimes irregularly lobed. Drupe bright red or orange, nearly globose, compressed, crowned with the remnant of the style. Seed more or less lenticular, black beneath “hairy” covering derived from pericarp, minutely arillate. Embryo annular, the cotyledons convolute. Endosperm persisting as a cap around the radicle. Megagametophyte (embryo sac) fundamentally of the *Polygonum* type, although the antipodal cells sometimes proliferating. TYPE SPECIES: *R. humilis* L. (Name commemorating Augustus Quirinus Rivinus (Bachmann), 1652–1723, professor of botany, medicine, and chemistry at Leipzig, early user of binomial nomenclature.) — BLOODBERRY, ROUGE PLANT, BABY PEPPER.

A single polymorphic species ranging from mid-Argentina northward across South and Central America and the West Indies to Mexico and the southern United States; introduced into warm regions elsewhere, including Africa, Asia, Australia, Madagascar, the Malay Archipelago, and scattered islands in the Atlantic and Pacific. In the continental United States, *Rivina humilis* is found across most of Florida and in Louisiana, Arkansas (*fide* Smith), Oklahoma, Texas, New Mexico, and Arizona. I have seen no documentation of the occurrence of *Rivina* in Mississippi or Alabama. It is naturalized in Hawaii.

Rivinas are herbaceous or shrubby, often conspicuously woody only at the base, and sometimes sprawling. Branching tends to be divaricate; often multiple axes arise from a single node. Pubescence is absent or variable. Diverse in shape and size, the leaf blades are frequently deltoid. The small flowers bear four stamens alternating with four tepals. The single compressed carpel is topped with a well-defined, curved style inserted obliquely and generally off center, and the stigma is capitate or lobate. The most outstanding characteristic is the bright reddish, juicy fruit containing one lenticular and "hairy" endocarp.

Rivina has been collected from dunes, rocks, cliffs, waste grounds, stream beds and banks, prairies, roadsides, thickets, seashores, canyons, swampy meadows, hammocks, and "dense," "wet," and "rain" forests. It invades cultivated areas. Sites are frequently shaded but also may be open—some are rich and moist, others dry. Flowering proceeds year-round in Florida.

By excluding *Trichostigma* and by broadening species concepts, modern monographers reduced the number of species in *Rivina* as compared with nineteenth century treatments. Walter (1909) recognized *R. humilis*, *R. portulacoides* Nutt.,¹¹ and *R. purpurascens* Schrader, separated in his key by the relative lengths and degrees of erectness of the inflorescences and by the colors and lengths of the tepals. Nowicke (1968), H. Harms (note in Heimerl, 1934), Standley, and others perceived only one species, for which Raeder listed 37 synonyms. Agreement is general that Walter's (1909) division of his already narrowly defined *R. humilis* into three plus the typical varieties based chiefly on pubescence is excessive splitting (discussion in Raeder).

Repeated counts have yielded $2n = 108$ as the chromosome number for *Rivina humilis*. Joshi's illustration reveals the chromosomes to be short and of fairly uniform length at diakinesis.

Pollen grains from one collection¹² of *Rivina humilis* show that discrepancies in the literature relating to numbers of colpi result from insufficient sampling. Most grains in this collection have five equatorial colpi plus five perpendicular colpi encircling each pole. Also common are grains with 12 colpi arranged similarly, but in fours. Scanning electron micrographs in Bortenschlager show microspines on the tectum and perforations in the endexine.

Nuclei in cells from *Rivina humilis* contain rod-shaped or short-prismatic

¹¹Although in Nuttall's protologue "*R. portulacoides*" does not sound in some respects like a species of *Rivina*, a specimen so named and labeled "Verdigris" from Nuttall's herbarium at BM is clearly *R. humilis*.

¹²Harvard Palynological Collection, slides 344, Texas, 1936.

protein bodies in clusters of up to 10 near nucleoli. As described by Carniel, these may be solid, hollow, or septate and are composed of granular subunits.

Kajale (1954a) determined that cells of the inside ovarian hypodermis elongate radially and differentiate into hairs between the outer tissues of the ovary and the inside epidermis, with the latter adhering to the seed coat. Hence the seed remains covered with a thin shaggy coat after the bulk of the pericarp falls away. (Netolitzky interpreted the "hairy" covering as belonging to the outer integument.)

Because of its attractive divaricate pattern of branching and bright red fruits, *Rivina humilis* is sometimes cultivated as an ornamental, a use dating as far back in Europe as the late seventeenth century. From the very little information that is available, the fruits and other parts are considered toxic (Burlage, Perkins & Payne, Lampe & Fagerström). *Rivina* taints milk of cows that eat it (White). Medicinal uses are listed in Ayensu and in Morton. Red juice from the fruits is said to have been used for dyeing, as rouge and ink, and for coloring cut flowers.

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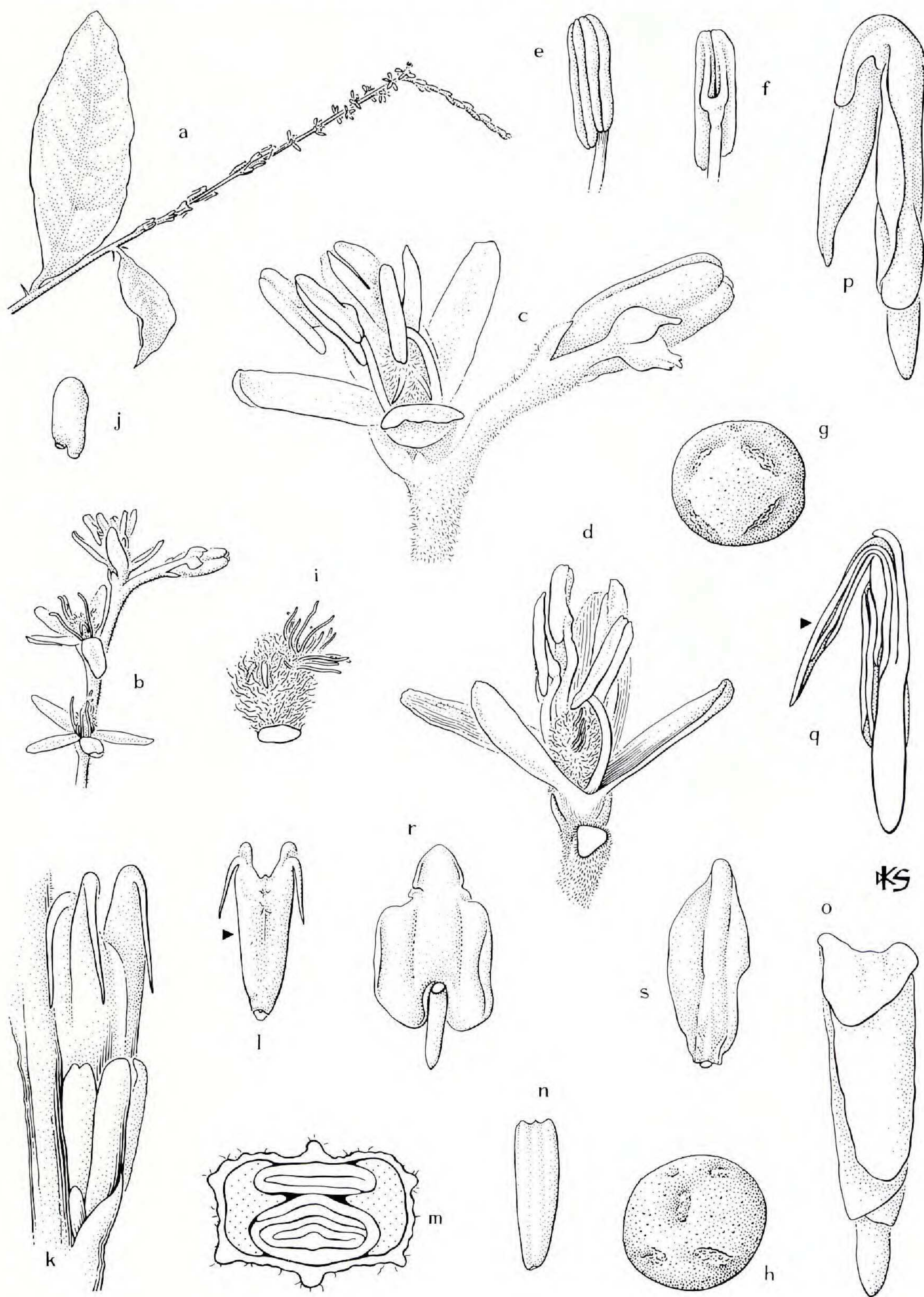
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4. **Petiveria** Linnaeus, Sp. Pl. **1**: 342. 1753; Gen. Pl. ed. 5. 160. 1754.

Herbs, subshrubs, or shrubs, sometimes sprawling, thickening by successive cambia (in root only?). Multiple shoots rising from 1 sometimes rhizomelike root. Branching sparse, multiple axes occasionally branching from 1 node. Plants with garliclike odor. Axes of inflorescences, young stems, petioles, and major foliar veins usually puberulent or tomentose to pilose or villous, additional organs also sometimes pubescent (abaxial surfaces of leaf blades often densely so). Calcium oxalate present primarily as styloid crystals. Leaves petiolate, the blades mostly elliptic to oblanceolate, infrequently rounded to usually acuminate at both ends, often apiculate at the apices; stomata usually with irregular subsidiary cells parallel to the guard cells. Axillary buds flanked by 2 stipulelike (probably foliar) bristles. Inflorescences axillary or terminal, composed of 1 or more long, thin, wandlike, uncrowded spicate axes tending to nod with the apogee of the bend near the youngest open flower, more erect in fruit; when branched, with a small number of lateral axes inserted toward the base of the similar main axis; bracts small, ovate-lanceolate to deltoid, the 2 bracteoles minute. Flowers nearly sessile, zygomorphic, ascending. Tepals 4, glabrous or pubescent abaxially at the bases, elliptic-oblong to narrowly lanceolate or narrowly deltoid, slightly connate basally and slightly adnate to bases of filaments, white or tinged with yellow, green, or pink, becoming green and erect in fruit. Stamens 4–6(–8), unequal, shorter than to about as long as tepals; anthers cleft at both ends. Pollen grains spheroidal or nearly so, 12- (or 15-)colpate [or 12-porate], or reportedly sometimes acolpate, the tectum spinulose and without punctate perforations (*fide* Bortenschlager). Gynoecium unicarpellate; ovary densely pubescent, bearing a set of hooks at the apex (these

FIGURE 3. **Petiveria**. a–s, *P. alliacea*: a, tip of stem with inflorescence—note bend in rachis at point where flower at anthesis, $\times \frac{1}{2}$; b, tip of inflorescence, showing anther-bearing flower at bend, 2 flowers after anthers have fallen (below), and flower buds (above), $\times 3$; c, detail of tip of inflorescence in "b"—note 2 hooks on ovary, $\times 10$; d, adaxial view of flower—note stigma on ovary (unshaded triangular area indicates scar where younger portion of inflorescence removed), $\times 10$; e, f, adaxial and abaxial views of anthers, $\times 12$; g, h, polar and equatorial views (respectively) of pollen grains, pollen 12-colpate with 4 colpi around each pole and 4 perpendicular to the polar colpi around the equator, $\times 1000$; i, side view of gynoecium, style absent, stigma penicillate—



note 2 hooks to left, $\times 12$; j, ovule, attachment point indicated by open circle at bottom left, $\times 12$; k, nearly mature fruit (an achene), with hooks above and persistent tepals below, $\times 5$; l, adaxial side of mature fruit, $\times 3$; m, cross section of fruit at level marked by arrows in "l" and "q," perisperm even-stippled, $\times 12$; n, seed, removed from achene, $\times 3$; o, abaxial surface of embryo, $\times 6$; p, side view of embryo, $\times 6$; q, vertical section of embryo, $\times 6$; r, embryo with longer (inner) cotyledon removed and shorter (outer) one unfolded, $\times 3$; s, unfolded longer cotyledon of embryo in "r."

enlarging considerably in fruit); style absent; stigma penicillate, facing the rachis; ovule straight, the micropyle alongside the funiculus. Fruit dry, indehiscent, cuneiform, longitudinally ribbed, pubescent, armed apically with 4 (or 5) [–13] sharp, stout barbs inserted on 2 lobes and bent back along the surface of the fruit for ca. $\frac{1}{4}$ – $\frac{1}{2}$ its length, sometimes with an extra, straight barb rising vertically between the lobes. Seed shaped like the fruit, the testa thin. Embryo with the cotyledons unequal, one wrapped around the other: the outer markedly auriculate basally, wider and shorter than the inner, this rolled into a tube; embryo bent double at about the middle of the inner cotyledon and near the apex of the outer one. TYPE SPECIES: *P. alliacea* L. (Named for James Petiver, ca. 1660–1718, British naturalist and apothecary, Fellow of the Royal Society, noted collector and prolific author.) — GUINEA-HEN WEED, GARLIC WEED.

One variable species distributed across most of Florida and occurring from southern Texas southward through Mexico, Central America, the West Indies, and South America to approximately Buenos Aires, Argentina. *Petiveria alliacea* has escaped from cultivation to a limited extent in warm parts of the Old World.

Long, slender, uncrowded, unbranched or sparsely branched, spicate inflorescences allow recognition of *Petiveria* from a distance. Fresh plants have a skunky or garlicky odor when injured. The small, four-tepaled flowers have a variable number of unequal stamens and a distinctive, densely pubescent ovary bearing hooks at the apex but no style. The brushlike stigma is more or less lateral. The unmistakable long, narrow, tapered, dry fruit is topped by four or more stout hooks. The odd bent embryo has two unequal cotyledons, one wrapped longitudinally around the other.

Investigating different sets of characters, Baillon and Walter (1906) each uncovered evidence suggestive of affinity between *Petiveria* and *Monococcus*. Baillon encountered similarities in vegetative organs, inflorescences, floral organization, and general construction of the embryos. Walter observed that the completely straight (*gerade*) ovules of the two distinguish them together from other Rivineae, in which the funiculus is inserted at the middle of the transversely overlaid nucellus (see Mauritzon for embryological details of *Petiveria*). Walter also mentioned that both genera have tepals overlapping so that one is outside at both edges, one is inside at both edges, and two have one edge inside and the other outside (a trait that reappears in Seguierieae). Further, in 1909, he mentioned similarity in their “*Stipularorgane*,” their seed coats, and the general forms of their embryos.

Petiveria differs from *Monococcus* in having perfect (vs. imperfect or polygamous) flowers rotated 45 degrees relative to those of *Monococcus*, spines terminal on (vs. covering) the fruits, fewer stamens, longer fruits, more dissimilar cotyledons, less nutritive tissue in the seed (see especially Baillon), and possibly anomalous secondary growth. (*Monococcus* probably lacks anomalous secondary growth; this is restricted to the root in *Petiveria* according to Holm, 1915; see also Metcalfe & Chalk, and Walter, 1909.)

Among the diverse habitats occupied by *Petiveria* are wet, tropical, evergreen forests, thickets, fields, and even savannas. Soils may be rich or not. Disturbed

sites, such as banks of streams, are common. Habitats reported in Florida, where *P. alliacea* flowers year-round, include cultivated land, waste places, hammocks, moist woods, and the top of a limestone cliff. This species at times becomes a weedy pest.

Distribution by animals is clearly effected by the hooks on the fruits. Ormond & Pinheiro (1974) induced autogamy in Brazilian specimens.

In 1909 Walter recognized *Petiveria tetrandra* Gomes as a distinct species, in his key distinguished from *P. alliacea* by six (vs. four) hooks on the fruits, glabrous inflorescence axes (a very unreliable character), and shorter tepals. *Petiveria tetrandra* is centered in or restricted to southern Brazil, northern Argentina, and Paraguay. Hauman-Merck and Nowicke (1968) reduced it to a variety of *P. alliacea*; after studying it at the heart of its range, Santos & Flaster and Hatschbach & Guimarães denied it any taxonomic status. As the result of a multifaceted investigation focused on the problem of the status of *P. tetrandra* and utilizing populations in Brazil, Ormond & Pinheiro (1974, 1975) tentatively advocated maintaining *P. alliacea* var. *tetrandra* (Gomes) Hauman-Merck. The subgroup they cautiously thought to correspond to var. *alliacea* differed from the one they believed probably to represent var. *tetrandra* in having a somatic chromosome number of 72 (vs. 36), four hooks per fruit (vs. 5 or more¹³), and several organs larger, as well as in other ways. The two entities remained phenotypically distinct under uniform cultivation. Crosses in both directions yielded some fruits, a result requiring careful interpretation in view of the alleged difference in chromosome number. Nowicke (1968) raised the possibility of apomixis by suspecting partial sterility in var. *tetrandra* as indicated by apparently acolpate pollen "notwithstanding the setting of fruit" (p. 344). Complicating the palynological picture, Bortenschlager observed porate grains in "*P. tetrandra*" and grains with elongate apertures in "*P. alliacea*."

The alliaceous odor that gave *Petiveria alliacea* its name, and the enthusiasm for this species in folk medicine, underscore the desirability of chemical studies. Pietschmann obtained evidence of mustard oils in roots and stems, and various other authors have ascribed them to the genus. However, Ettlinger & Kjaer dismissed Pietschmann's evidence as "meaningless"; their own tests on the garlicky seeds were negative for myrosinase and glucosinolates. The odor most likely comes from sulfur-containing compounds other than mustard oils: Von Szczepanski and colleagues established an antimicrobial oil from roots and stems of *P. alliacea* as benzyl-2-hydroxyethyl-trisulfide; Adesogan characterized another sulfur-containing compound from the roots as *cis*-3,5-diphenyl-1,2,4-trithiolan ("trithiolaniacin"). Segelman & Segelman isolated isoarborinol, related compounds, and potassium nitrate from leaves. (For the chemistry of *Petiveria* see also Dias da Silva, Hegnauer, Loustalot & Pagán, Rocha, and Rocha & Da Silva.)

¹³Specimens displaying the sharpest distinguishing trait of *P. alliacea* var. *tetrandra*, more than four hooks per fruit, occur beyond the boundaries given above. For example, fruits on *Bartlett 10787* (GH) from Mexico have 4, 5, or 6 hooks.

In view of the odor, antimicrobial properties, reputed narcotic effects (Dias da Silva), noxiousness, and toxicity (see symptoms of poisoning in Peckolt & Peckolt) of *Petiveria alliacea*, it is unsurprising that plants of this species are valued and sometimes marketed as a folk remedy. Its attributed benefits are available in numerous references, among them Ayensu, Dias da Silva, Morton, Peckolt & Peckolt, Sorarú & Bandoni, Standley, and Wong. This species is reputed to degrade the milk and meat of cattle, in which it also induces abortion. (The last-mentioned effect applied to humans is one of the most frequently mentioned medicinal uses.) Griffith recounted that a nauseating infusion of roots of *P. "foetida"* in rum was employed in the West Indies to instill disgust for liquor. Somewhat insecticidal, *Petiveria* has been used to free woolen goods and chickens of vermin. Harms (note in Heimerl, 1934) and the label of the Brazilian collection *Krukoff's 6th Expedition . . . 7638 (A)* mentioned *Petiveria* as an ingredient in curare poison. As related by Peckolt & Peckolt, *P. alliacea* has been used to poison fish. The hooks on the fruits can puncture human skin.

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Subfamily AGDESTIDOIDEAE Nowicke

5. **Agdestis** Moçônio & Sessé ex A. P. de Candolle, *Syst. Nat.* **1**: 511, 543. 1817 (“1818”).

Slightly woody, twining, pungent-smelling vines, sometimes with large napiform taproots. Sieve-tube plastids with globular crystalloids. Plants puberulent on axes of inflorescences, abaxially on leaf blades, and sometimes lightly on young stems. Calcium oxalate present primarily as raphide bundles. Leaves petiolate, the blades suborbicular to usually cordate, rounded to acute and often mucronate apically, often about as wide as long; slender petioles about as long as leaf blades; stomata anomocytic. Inflorescences mostly axillary, sometimes terminal, lax, composed of main axes bearing simple or compound lateral dichasia, or bearing single flowers in axils of bracts (some axes exclusively with such single flowers), or bearing branches resembling the main axes; bracts and bracteoles inconspicuous, subulate to lanceolate. Flowers perfect, pedicellate, strongly scented. Tepals 4 (5 or rarely more), white, elliptic or oblong to oblanceolate, separate or slightly coalescent basally. Stamens 15–30; filaments slender, unequal, shorter than to slightly longer than tepals, threadlike, inserted

irregularly; anthers cleft at both ends. Pollen grains subspheroidal to subprolate, tricolpate, the tectum spinulose and punctate-perforate. Gynoecium syncarpous; ovary semi-inferior, (3- or) 4-locular; stigmatic lobes (3 or) 4, thick, papillose adaxially, recurved, shorter than to slightly longer than the single conical, stocky style. Fruit small, dry, indehiscent, obconical, ribbed, surrounded by the enlarged, greenish, spreading, winglike, prominently veined tepals, unilocular and 1-seeded by abortion. Seed with thin testa adherent to pericarp. Embryo annular, the cotyledons linear, slightly wider than radicle. TYPE SPECIES: *A. clematidea* Moçinho & Sessé ex A. P. de Candolle. (Named for a disagreeable hermaphroditic monster because of the anomalous original position of the plant in the dioecious Menispermaceae.¹⁴)

A single species distributed from Texas southward through Mexico to Guatemala, reported from Honduras and Nicaragua, and escaped from cultivation in warm places elsewhere. *Agdestis clematidea* is cultivated at least as far north as Jacksonville, Florida, and occurs outside of cultivation in disturbed sites and hammocks in the southern half of Florida.

Several distinctive attributes allow ready recognition of *Agdestis* and isolate it from other Phytolaccaceae. It is a slender vine capable of forming dense tangles and climbing over shrubs and high into trees. (Taylor estimated growth to be as fast as 40 or 50 feet per year.) The turnip-shaped taproot protrudes above the surface of the ground and, according to Taylor, may weigh as much as 150 pounds (Heimerl, 1934, says six pounds). The cordate leaf blades are highly distinctive. Observers describe odors from the foliage and root as garlicky, skunklike, reminiscent of cabbage, or fetid. Descriptions of the floral scent include "very sweet-scented" (Taylor) and "more fetid than those of the carrion-flower or skunk-cabbage" (Britton). Mexia (8947, GH) recorded the stench to have caused headaches. The white flowers in simple or compound dichasia (vs. mostly racemose inflorescences in other Phytolaccaceae) each have four tepals, generally four stigmatic lobes on one compound style (most Phytolaccaceae have one style per carpel), and usually four locules in the ovary, with three aborting. The partly inferior ovary is unique in the family. The single seed adheres to the pericarp of the small indehiscent fruit encircled by spreading tepals.

Bortenschlager found *Agdestis* to agree palynologically with other Phytolaccaceae. While not favoring affinity with Phytolaccaceae in particular, the presence of betalains and P-type sieve-tube plastids confirms *Agdestis* as a member of the Centrospermae (Behnke *et al.*, 1974).

The morphological peculiarity of *Agdestis* is reflected in the taxonomic positions assigned it by different authorities. Most regard *Agdestis* as an isolated member of the Phytolaccaceae. Walter (1909) listed it among *genera anomala*; Heimerl (1934) treated it as the sole genus of tribe Agdestideae Heimerl; and Nowicke (1968) established for it the monogeneric subfamily Agdestidoideae

¹⁴According to one version of the Phrygian myth, Cybele—embodied as the Agdus Rock—gave birth unwillingly to Agdestis despite her having thwarted rape by Jupiter. Blood that spilled when the gods tricked the arrogant Agdestis into drunkenness and bound him/her to a tree spawned a second tree, this yielding fruits responsible for the conception of Attis in the princess Nana.

Nowicke. Hutchinson recognized it as the single member of the Agdestidaceae Nakai.

Agdestis resembles other Phytolaccaceae in its weediness, preferring naturally and artificially disturbed sites. It grows in such diverse habitats as tropical forests, dry thickets, rocky places, and clearings.

Ridley (p. 111) observed that a number of taxonomically disparate woody climbers of "rather open jungles in the tropics" produce usually small, one-seeded fruits surrounded by spreading winglike sepals that cause the fruit to rotate rapidly while falling. Among his examples is *Agdestis*. That the falling fruits indeed whirl like the blades of a helicopter is readily demonstrated with fruits from herbarium specimens.

Observations on the nature of secondary growth are contradictory, with the balance tipped toward the presence of successive cambia (*cf.* Cobau; Heimerl, 1934; Metcalfe & Chalk; Walter, 1909).

Agdestis has limited application as an ornamental in circumstances where its odor is not objectionable. It forms a thick cover sometimes used to decorate buildings and hide eyesores.

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